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DArTseq-based genome-wide SNP markers reveal limited genetic diversity and highly structured population in assembled West African cowpea germplasm

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ABSTRACT

The potential of cowpea (*Vigna unguiculata* [L] Walp) to contribute to food security and livelihood sustenance of sub-Sahara Africans is constantly threatened by many biotic and abiotic stresses that are aggravated by climate change. To address these threats, cowpea breeding programs in the subregion prioritize climate-resilience traits and resistance to biotic stresses. However, before successful trait discovery and implementation, it is essential to characterize diversity and population structure of cowpea germplasm. To test the hypothesis that assembled cowpea germplasm exhibits limited and narrow genetic diversity with a well-defined population structure, we assessed the level of genetic variability and characterized the population structure of 188 cowpea genotypes using 5147 Single Nucleotide Polymorphism (SNP) markers. The structure results revealed five major genetic groups with moderate levels of genetic diversity and an admixture level of 17 %. Discriminant analysis and phylogenetic analysis supported this finding, indicating the presence of distinct groups within the cowpea population. The analysis of molecular variance (AMOVA) showed 27 % among population variance, 64 % within-population variance, and 9 % within individual variance. While considering the origin, the AMOVA showed 16 % among population variance, 75 % among individual variance, and 9 % within individual variance. This study provides valuable insights for future cowpea improvement programs by facilitating the selection of suitable progenitors for population development, and contributing in the conservation of cowpea genetic resources. Addressing these challenges and enhancing cowpea's diversity and resilience are crucial steps towards ensuring food security and sustainable livelihoods in sub-Saharan Africa.

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Introduction

Cowpea (*Vigna unguiculata* [L.] Walp.) is one of the most important legume crops in sub-Saharan Africa (SSA), known for its cheap source of protein for the rural-urban populace and livestock with additional advantage in its ability to fix nitrogen to improve soil fertility [1,2]. Cowpea grains are highly nutritious, consisting of 63% carbohydrates, and 25.0% protein, with low-fat content, and are rich in vitamins (A, B1, B9, C), a range of minerals (Ca, P, Fe), folic acid, riboflavin, and thiamin [3]. Globally, more than 8.9 million tons of dry cowpea grains were produced in 2021 on a minimum of 14 million hectares planted all over the world. In Africa, particularly West Africa, 74.3% of the world's cowpea production takes place on 82.8% of this land area. Nigeria is the world's largest producer of cowpea, followed by Niger, Burkina Faso, Cameroon, Ghana, and Mali [4].

In SSA, cowpea is cultivated as a sole crop or in association with pearl millet, sorghum, and maize under rain-fed conditions. For the last two decades, cowpea production has shown a steady increase due to the increase in the land area rather than the increase per unit of land area [5]. The average cowpea yield of the top three producers in West Africa ranges between 0.25 – 0.75 t/ha, which is much lower than the 2.00 t/ha reported in the United States of America [4]. This significant reduction in cowpea yields in West Africa is attributed largely to abiotic and biotic stresses [6,7]. To address these yield-limiting threats, cowpea breeding programs in the sub-region strongly feature climate-resilience traits and resistance to biotic stresses in their product profiles. Developing improved climate-smart cowpea varieties with higher yields and better nutritional value would be beneficial to both small-scale and commercial farmers in the subregion. However, as a prerequisite for successful trait discovery and delivery to cowpea breeding pipelines, assembled germplasm for cowpea improvement must be characterized to unravel its diversity and population structure. Self-pollination is a key factor that limits gene flow and leads to narrower genetic base in cultivated cowpea varieties [8]. Thus, it is necessary to assess the genetic diversity of cowpea to make the best use of available germplasm, protect it and guide crop improvement projects. For successful breeding programs, it is very important to have an adequate amount of genetic diversity [9,10].

One of the reliable methods of assessing genetic diversity reported by many researchers is the use of molecular markers as they are not affected by plant developmental stages or the environment [11,12]. Of the molecular markers, Single Nucleotides Polymorphism (SNP) markers from Next Generation Sequencing platforms (NGS) have been reported as the most efficient marker system for diversity assessment [13]. Of the NGS platforms, the Diversity Array Technology sequencing (DArTseq) platform has an advantage over other methods in parallel sequence data analysis compared to other platforms and sequencing genomes without the need for sequence information. To this end, DArT markers derived from NGS represent prime alternative for diversity studies due to their comprehensive genomic coverage, with high throughput, and cost-effective advantage [14,15]. Numerous researchers have used DArTseq markers to explore the genetic relationship in cowpea lines. Togolese cowpea accessions from six different sources or origins were successfully grouped into four distinct groups with an average genetic distance of 0.31 using DArT markers [15]. Three distinct genetic populations were identified from 768 globally collected cowpea genotypes [16]. The phylogenetic analyses between each individual, region, and country revealed the potential ancestral regions (East and West Africa) and identified the migration patterns and the historical process of cowpea dispersal and development [16]. DArTseq technology has also been extended to other crops [16]. The aim of this study is to assess the genetic diversity and population structure of 188 cowpea germplasm from west Africa using DArTseq-derived Single Nucleotide Polymorphism (SNP) markers.

Materials and methods

Plant material

The 188-cowpea germplasm used for this study consists of accessions that were obtained from five top producers of cowpea in West Africa, including Nigeria, Niger, Ghana, Burkina Faso and Senegal. But also, two accessions from US, eight from Uganda and four from India (table S1: the country of origin of 188 cowpea accessions, and seed color). Inclusive in the cowpea germplasm were farmers preferred varieties collected and kept in gene banks and breeding lines from various research institutes. These accessions were established on a row plot size of 2.2 m each in 2021 for leaf sample collection and performance evaluation at Manga Research station, Bawku, Upper East, Ghana. Four weeks after planting, 100 mg of young trifoliate leaves were collected on one plant per accession and placed in a ziplock bag containing 20 g of dried silica gel. All samples were kept in a dark room condition for drying. Dried leaf sample (20 mg) was placed into Eppendorf tubes for each accession, packaged, and sent to the Diversity Arrays Technology Pty, Ltd, Canberra, Australia for genotyping services.

Genotyping and SNP data analysis

DNA extraction from each leaf sample was performed according to DArT internal protocol (last observed online 10 November 2022) (https://www.diversityarrays.com/services/laboratory-services/dna-extraction/). The quality of the DNA was checked through visual inspection on 0.8 % agarose gel, as well as quantitative analysis using a Nanodrop 2000c spectrophotometer (Thermo Scientific, Waltham, Massachusetts, USA). The DNA genotyping was carried out with DArTseq Technology (https://www.diversityarrays.com/technology-and-resources/dartseq/) and the genomic DNA library was created through genomic complexity reduction. After that, automated clonal amplification (cBot Illumina) and sequencing (NGS on illumine Hiseq2500/Novaseq) with 1200,000 reads per sample was run. The reads were mapped against the cowpea IT97K-499–35 reference genome *Vigna unguiculata* v1,1 from Phytozome website (https://phytozome.jgi.doe.gov/pz/portal.html#!info?alias=Org_Vunguiculata_er). The raw HapMap file generated from

DArT was subjected to SNP.QC in R using the quality control criteria of low sequence depth <5; SNP markers with missing values >20 %; minor allele frequency (MAF) <0.05 and heterozygosity >50. Of the 14,154 SNP markers subjected to quality control, 5147 highly informative SNP markers were retained for downstream analysis (table S2: Genotypic data of 188 cowpea genotypes, collected in West Africa, India, Uganda and USA).

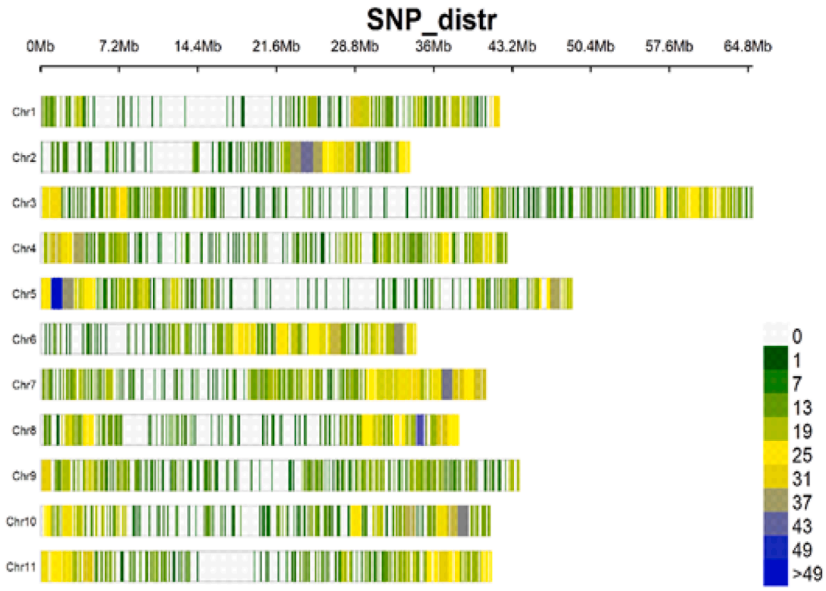
Genetic diversity and population genetic analysis

The minor allele frequency (MAF), major allele frequency (MAF), gene diversity (GD) or expected heterozygosity (He), observed heterozygosity (Ho), polymorphic information content (PIC) and inbreeding coefficient (FIS) for each locus were obtained using the PowerMarker 3.25 software [17]. To determine the inherent population structure of the 188 cowpea accessions, a model-based clustering method was implemented using Structure Software version 2.3.4 [18]. The simulation was performed without prior information on the individuals with the number of expected sub-populations or cluster (K) varying from 1 to 10 with 5 replications. Each replication was run with no prior information on the origin of individuals and iterations and burn-ins set to 100,000. The Evanno transformation method [19] was used to determine the most appropriate K-value within the set of cowpea accessions using Structure Harvester (https://tailor0.biology.ucla.edu/Structure/Harvester). Gene pool groups were assigned to cowpea accessions based on their membership probabilities, with any accessions having a probability of 0.80 or higher being assigned to their respective group. Those with a probability less than 0.80 were assigned to the mixed group and referred to as admixture. Population structure was further plotted using the bar plot function implemented in R. Discriminant analysis of principal component (DAPC) was also used to determine the optimal number of clusters using the find.cluster function implemented in R [20]. This function employs the k-means approach which run sequentially with increasing values of k, and compares different clustering solutions using Bayesian Information Criterion (BIC). The optimal number of clusters was identified from the lowest point showing an elbow joint on the BIC curve. Discriminant analysis was then performed on the retained principal components using the dapc function in adegenet package [21] implemented in R. Lastly, the phylogenetic analysis was done using the Gower distance calculated after converting the filtered SNP results into numerical format in GAPIT 3 [22]. The phylogenetic analysis using the Analysis Phylogenetic and Evolution package [23] was used to understand the segregation pattern of the 188 accessions with the largest country of origin as a cofactor. The dendrogram was plotted using the ggtree package [24]. Analyses of Molecular Variance (AMOVA) and genetic differentiation (F_{ST}) were used to estimate the explained genetic variances among and between the populations of cowpea accessions using GenAIEx 6.5 [25].

Results

SNP markers distribution across cowpea genome and diversity

The SNP marker distribution revealed that chromosome three has the highest number of SNP markers while chromosome one has the lowest (Fig. 1). The marker alleles observed were A/G (28.52%) C/T (28.35%), A/T (11.85%) G/T (10.65%), A/C (11.35%) G/C (11.26%) (Table 1). A larger transition-type SNP level (56.87%) was observed compared to transversion-type SNPs level (43.13%) in the cowpea genomes thus giving a ratio of 1.32:1. The marker diversity indices showed an average MAF of 0.19 with a range of 0.01 to



Chromosome	Number
1	324
2	368
3	620
4	487
5	496
6	470
7	570
8	420
9	406
10	490
11	496

Fig. 1. Distribution of 5147 SNPs across the cowpea chromosomes.

0.5 respectively. The expected heterozygosity (He) averaged 0.26 with a minimum and maximum of 0.02 and 0.50 respectively while the observed heterozygosity (Ho) averaged 0.33 with a minimum and maximum of 0.01 and 0.66 and Polymorphic Information Content (PIC) averaged 0.22 with a minimum and maximum of 0.02 and 0.38, respectively (Table 2).

Population structure of 188 cowpea accessions

Through the BIC analysis, population structure revealed the presence of deflection at k equal to 5 (Fig. 2a). Using 80 % membership probability threshold, 156 cowpea accessions (82.8 %) were successfully assigned to the five clusters while 32 (17.02 %) could not be assigned to any cluster and were designated as admixtures (Fig. 2b). The Gower genetic distance (GD) displayed the range of genetic distance from 0.005 between G11 and G09 to 0.280 between G98 and G04 with an average of 0.166. The Hierarchical clustering based on the DArT-SNP marker grouped the 188 cowpea accessions into five major genetic groups or clusters (Fig. 3). Fifty-six cowpea accessions were grouped in cluster one (blue) with the lowest GD (0.005) obtained between two pairs of cowpea accessions (G09 and G11, G115 and G114) and the highest GD obtained between G02 and G01 (0.190). Cluster two (green) has twenty-three cowpea accessions the lowest GD (0.006) found in four pairs of cowpea accessions (G55 and G49, G55 and G52, G55 and G53, G48 and G55) and the highest GD obtained between the accessions G159 and G56 (0.101). Cluster three (red) has the lowest number of cowpea accessions (14) with the lowest GD (0.006) between G163 and G148 while the highest GD was between the accessions G99 and G152 (0.188). Cluster four (purple) has the highest number of cowpea accessions (74) with the lowest GD (0.007) found between two pairs of cowpea accessions (G170 and G151, G86 and G188) while the highest GD was between the accessions G63 and G90 (0.210). Cluster five (cyan) has 19 cowpea accessions with the lowest GD (0.033) found between the accessions G180 and G178 while the highest GD (0.183) was between the accessions G180 and G72. The average GD of the five genetic groups or clusters obtained were 0.093, 0.062, 0.120, 0.150, and 0.140 for genetic group one, two, three, four, and five, respectively (Fig. 3). The DAPC analysis also revealed five clusters as observed for BIC and Hierarchical clustering-based analyses. In this grouping, clusters four and five showed a higher level of similarity while clusters one, three, and five showed high dissimilarity with these two clusters as well as among each other (Fig. 4).

Analysis of molecular variance of 188 cowpea accession using 5147 SNP markers

The AMOVA results based on the cluster captured the spread of genetic variation between and within the population groups (Table 3). The results showed among population variation of 27 %, 64 % variation among individuals within population, and 9 % variation within individuals. While the AMOVA results based on origin of collection of the 188 cowpea accessions revealed 16 % variability among origin, 75 % variation among individual within origin, and 9 % variation within origin. The pairwise differentiation among the origin of collection was highest between Burkina-Faso and Uganda (0.41) while the lowest was found between Ghana and USA (0.00) and Nigeria (0.01) (Table 4).

Hierarchical grouping of 188 cowpea accessions based on the country of origin

Using the Hierarchical clustering-based DArT-SNP method with consideration for country of collection or origin, the 188 cowpea accessions clustered irrespective of their origin of collection for most countries. About, 80% of the Senegal and Niger cowpea germplasm separated into different clusters. However, for the other countries, the cowpea germplasm separated irrespective of the country of origin (Fig. 5).

Discussion

In this study, 5147 SNP markers were used to evaluate the genetic diversity and population structure of cowpea accessions mostly from West African origin. A moderate level of genetic diversity was observed for the cowpea germplasm used for this analysis, indicating the extent to which germplasm exchange has taken place between these countries [26]. The population structure showed five different sub-populations with 17% level of admixture. The level of admixture could be a result of gene flow that was observed between some countries of collection. The introduction of breeding lines for population development which have a proportion of their genome derived from each of identified sub-population or clusters contributed to the level of admixture observed in the current study. Several studies on genetic diversity have been reported [27,28] however, few have employed the use of SNP markers on West Africa's cowpea germplasm [15,16].

Table 1
Percentage of DArT SNP type used in the current study.

SNP	Number	Percentage
A/G	1468	28.52
C/T	1459	28.35
A/T	610	11.85
G/T	548	10.65
A/C	534	10.37
G/C	528	10.26
Total	5147	100

Table 2
Diversity indices of 188 cowpea accessions based on 5147 DArTseq SNP markers.

Marker	MAF	He	Ho	PIC
Min	0.01	0.02	0.01	0.02
Max	0.50	0.50	0.66	0.38
Mean	0.19	0.26	0.33	0.22

MAF: minor allele frequency, He: expected heterozygosity, Ho: observed heterozygosity, PIC: polymorphism information content.

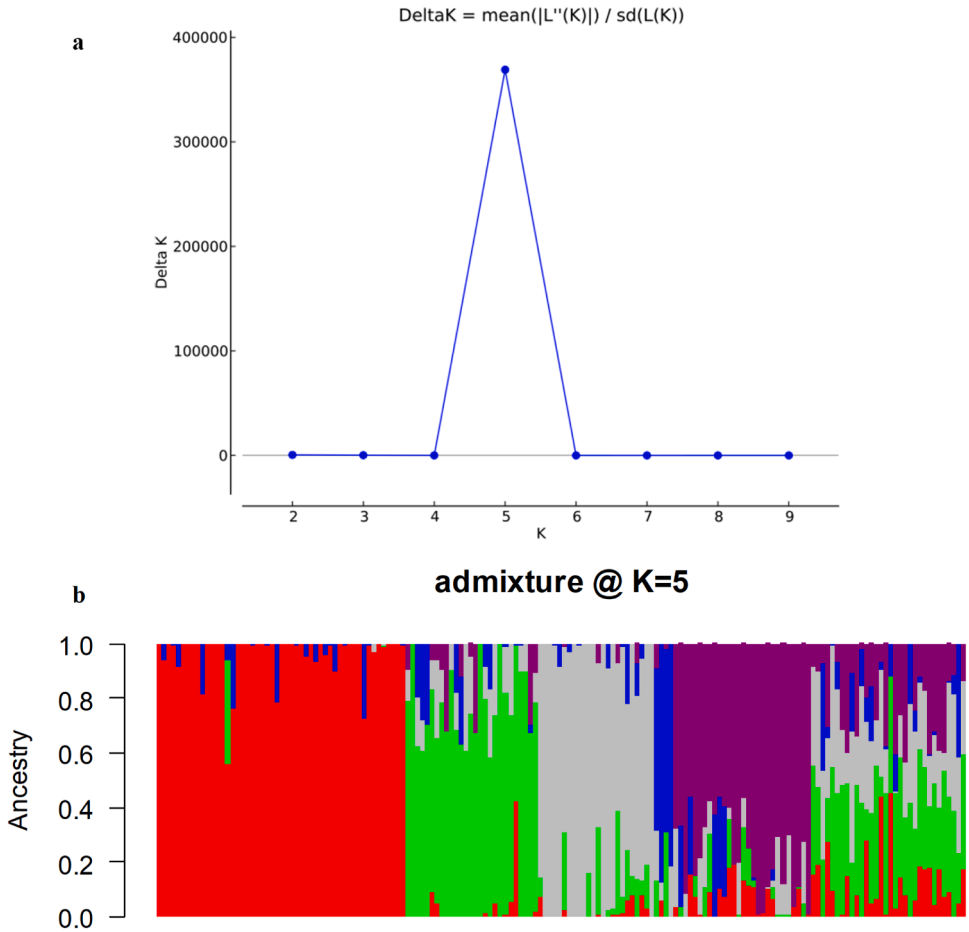


Fig. 2. (a) Population structure showing optimal delta $K = 5$; (b) with sub-population 1 in red, sub-population 2 in green, sub-population 3 in grey, sub-population 4 in blue, and sub-population 5 in purple colors, respectively for the 188 cowpea accessions using 5147 SNP markers.

In West Africa, where cowpea is grown more than in any other part of the world, mostly in the Savanna and the Sahel agro-ecologies owing to better adaptation to drought stress in low precipitation areas, our study revealed germplasm movement between West African countries [28,29], especially between Ghana and Nigeria. These two countries have shared a large number of cowpea accessions compared to any other origin of collection for cowpea germplasm studied. This could be attributable to their socio-cultural proximity and historical interactions. Ghana and Nigeria have also a long history of trade and cultural exchange which has facilitated the movement of agricultural produce and products, such as cowpea seeds across their borders [30]. The collaboration of researchers and farmers from the two countries has contributed to this exchange as well. Our study further showed that Ghana has also introduced cowpea accessions from other regions such as Burkina Faso, Senegal, Niger, Uganda, India, and the US.

The cowpea germplasm used in this study exhibited a SNP variation with A/G and C/T being most abundant compared to other SNP variants. This finding aligns with previous research results indicating that A/G and C/T SNPs are the most abundant in cowpea genome [15,16]. Furthermore, the transition/transversion ratio observed in this study, is in agreement with the results from many other cowpea researchers [15,26,31]. The low expected heterozygosity (0.26) are similar to that observed by Gbedevi et al. [15], Seo et al. [32] and Xiong et al. [16]. This is explained by the self-pollinated nature of cowpea with limited outcrossing. The inbreeding coefficient value approaching unity observed in this study suggest deficit of heterozygosity which is expected of the cowpea lines. The

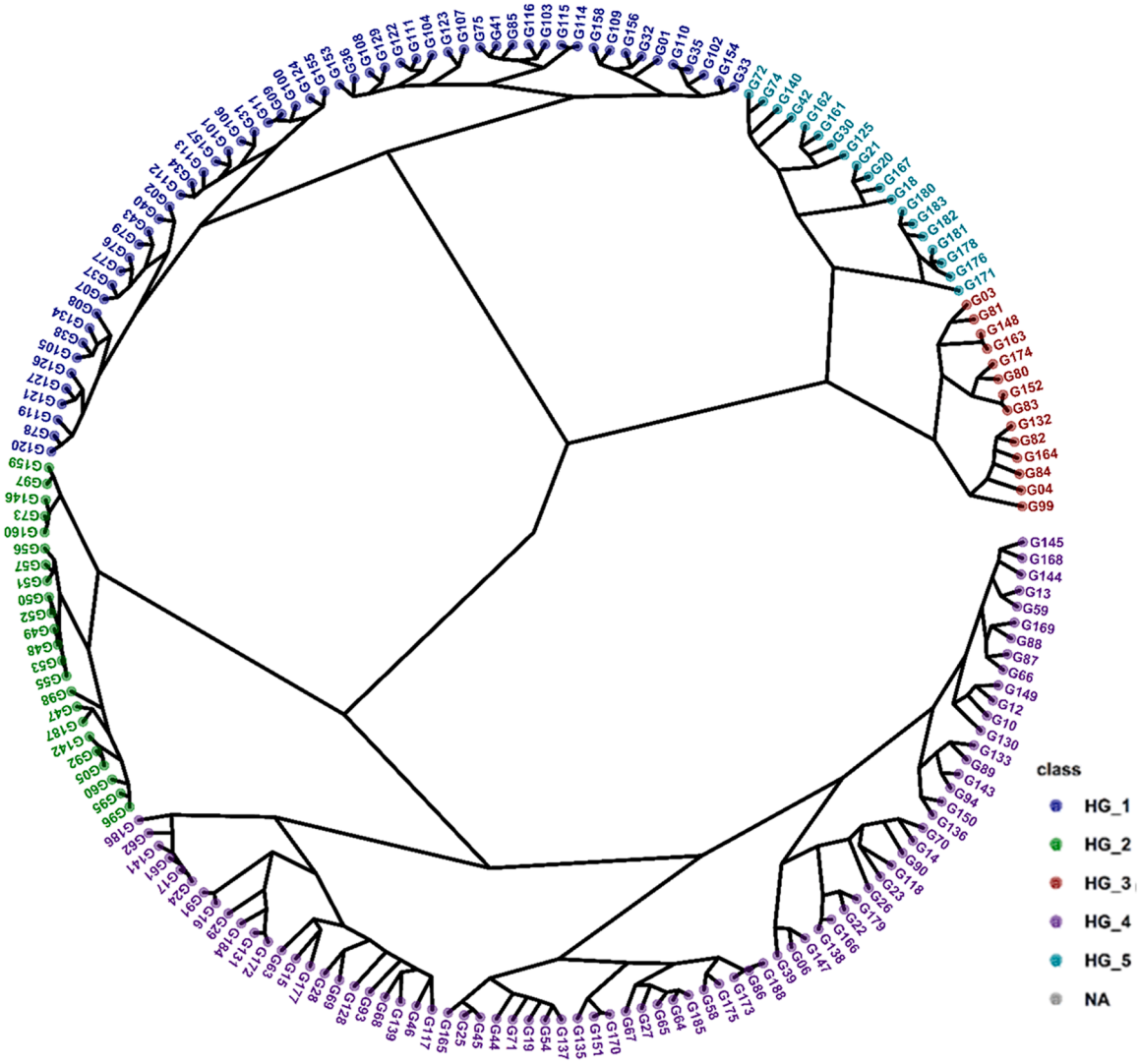


Fig. 3. Hierarchical clustering of 188 cowpea accessions from 5147 SNP markers revealed five genetic or cluster groups. genetic *group 1 (blue),* genetic *group 2 (green),* genetic *group 3 (red),* genetic *group 4 (purple), and* genetic *group 5 (cyan).*

mean PIC value of 0.22 observed suggests that the markers used are reasonably informative [32].

In the present study, high genetic variation among individuals within population and among populations showed the evidence for exchange of genetic materials. Gbedevi et al. [15] and Sarr et al. [33], reported similar findings in cowpea diversity studies in Togolese and Senegalese cowpea germplasm, respectively. Other authors that reported similar findings include Xiong et al. [16] and Mafakeri et al. [34]. However, Chen et al. [35], observed a higher within population variation (51.6 %). In their study on diversity assessment in the Chinese cowpea accessions, 25.1 % of the variation was attributed to differences within individuals while 23.3 % of the variation was observed among populations.

The gene flow among the origin of collection of cowpea accessions in this study was 1.350, indicating evidence of exchange of genetic material among the origin of the collection. The hierarchical clusters-based analysis and the discriminant analysis of principal components grouped the cowpea accessions into five major groups. Interestingly, the accessions tend to cluster together regardless of their geographic origin. The clustering pattern could be attributed to the common practice of farmer-to-farmer seed exchange, trade and sub-regional research programs exchange of germplasm which are prevalent in sub-Saharan Africa [36].

AMOVA results based on population structure and country of origin reveal that the variations among individual within populations accounted for the largest proportion of the total variation (64% and 75 %, respectively). The low to moderate level of diversity among populations could be linked to several factors, including the exchange of germplasm across regions. These findings are consistent with the results of numerous diversity studies conducted on cowpea collections utilizing various markers [11,26].

In our understanding of population differentiation (F_{ST}) according to [37,38], estimates between 0.00 and 0.05 suggests no to low levels of differentiation, between 0.06 and 0.15 indicates moderate levels of differentiation, between 0.16 and 0.25 indicates high

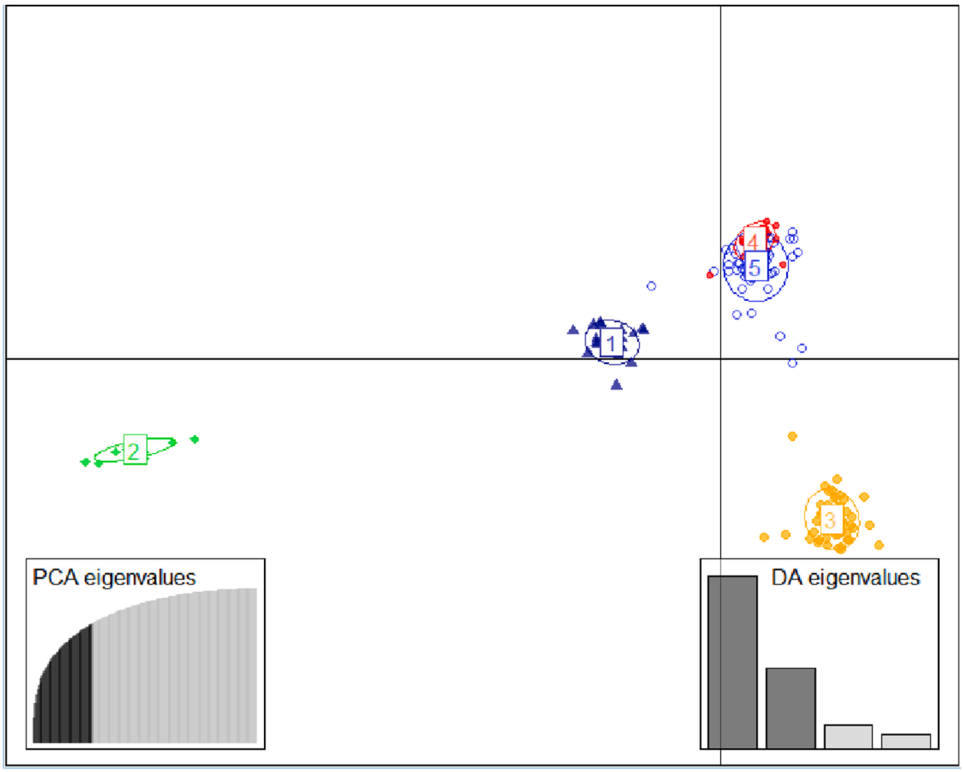


Fig. 4. Discriminant analysis of principal components of 188 cowpea accessions revealed five clusters from 5147 SNP markers.

Table 3
Analysis of molecular variance among 188 accessions assessed with 5147 SNP markers.

	Source	Df	SS	MS	Est. Var.	F statistics	PV
	Among Populations	4	75,588,477	18,897,119	256,387	F_{ST} =0.274	27 %
$K = 5$	Among Individual Within population	183	233,504,895	1,275,983	596,038	F_{IS}=0.877	64 %
	Within Individual	188	15,774,500	83,907	83,907	F_{IT}=0.910	9 %
	Total	375	324,867,872		936,332		100 %
	Nm	0.663					
	Among Origin	7	50,562.957	7223.280	140.739	F_{ST} =0.156	16 %
Origin = 8	Among Individual Within Origin	180	258,531.351	1436.285	676.189	F_{IS}=0.890	75 %
	Within Origin	188	15,774.500	83.907	83.907	F_{IT}=0.907	9 %
	Total	375	324,868.809		900.835		100 %
	Nm	1.35					

DF: degree of freedom, SS: Sum of Squares, MS: mean square, Est.Var.: estimated variance, PV= percentage variance. F_{ST}: Genetic differentiation, F_{IS}: fixation Index or inbreeding coefficient, F_{IT}: overall fixation index, Nm: gene flow.

Table 4
Pairwise differentiation of 188 cowpea accessions based on origin of collection.

	BF	Ghana	India	Niger	Nigeria	Senegal	Uganda	USA
BF	0.000							
Ghana	0.060	0.000						
India	0.195	0.029	0.000					
Niger	0.028	0.087	0.192	0.000				
Nigeria	0.095	0.010	0.024	0.109	0.000			
Senegal	0.237	0.142	0.128	0.234	0.147	0.000		
Uganda	0.405	0.228	0.160	0.376	0.237	0.278	0.000	
USA	0.088	0.000	0.021	0.108	0.029	0.193	0.357	0.000

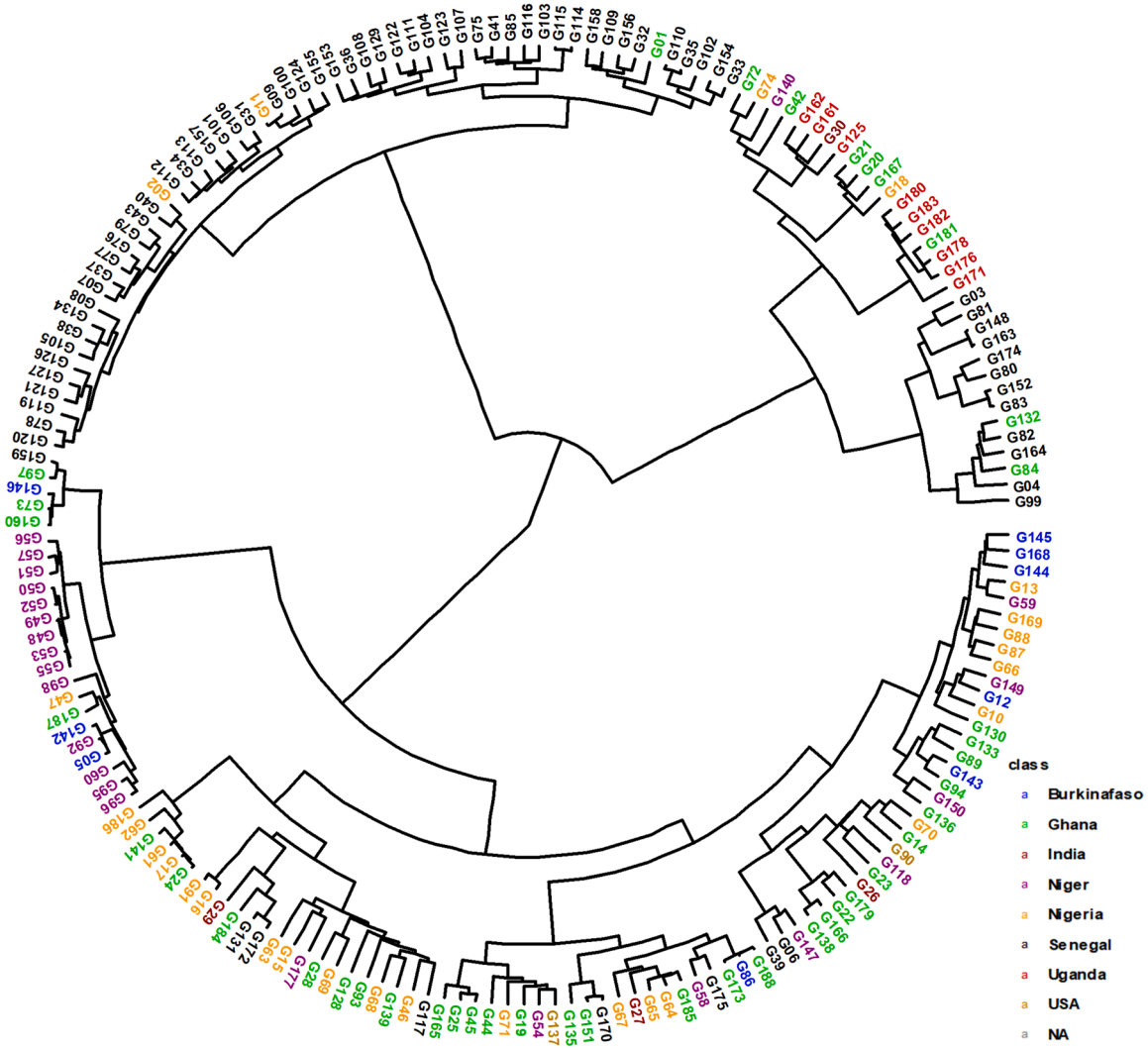


Fig. 5. Hierarchical clustering-based with consideration for country of collection or origin.

levels of differentiation, and estimates above 0.25 indicates a very high level of differentiation. In the assembled cowpea collection, we found pairwise F_{ST} values ranging from 0.00 to 0.405 indicating no to very high genetic differentiation among pairs where such estimates were observed. In pairs where zero estimates were found it indicated that the cowpea collections from such origins are similar or duplicated through germplasm transfer. When gene flow is greater than unity, it signifies a sufficient level of gene flow [37]. In the present study, the gene flow among various countries of origin is calculated to be 1.35, which indicates the presence of germplasm exchange among the country of origin used for the study. Our findings align with the previous reports on cowpea germplasm collected from diverse sources similar to this study [26,39].

Conclusion

This study observed five distinct genetic groups within the population of cowpea accessions with some of the accessions sharing high proportions of their genome across more than one distinct genetic group. Hierarchical clustering revealed that cluster groups are connected to respective origin of collection of the cowpea accessions with evidence of germplasm exchange expressed as gene flow and a moderate levels genetic diversity. Also, the pairwise F_{ST} values ranging from 0.00 to 0.405 highlighted low to very high of genetic differentiation among origin of collection. These findings have significance for cowpea enhancement across source countries, using these germplasms as breeding references. The genetic diversity observed within the germplasm collection would offer beneficial means for enhancing cowpea breeding programs in the sub-region.

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Availability of data and materials

Data can be obtained upon request from the corresponding author; available on aliabkoura@gmail.com

Declarations

Ethics approval and consent to participate.

CRediT authorship contribution statement

Abdoulaye Ali Koura: Conceptualization, Methodology, Software, Writing – original draft, Formal analysis. **Alexander Wireko Kena:** Conceptualization, Methodology, Software, Writing – review & editing, Formal analysis. **Benjamin Annor:** Supervision, Writing – review & editing. **Idris I Adejumobi:** Writing – review & editing. **Fanna Maina:** Writing – review & editing. **Abdoul- Raouf S. Maazou:** Writing – review & editing. **Ibrahim B.Y.A. Razakou:** Writing – review & editing. **Patrick Attamah:** Writing – review & editing. **Francis Kusi:** Supervision, Writing – review & editing. **Ousmane Boukar:** Supervision, Writing – review & editing. **Richard Akromah:** Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sciaf.2024.e02065.

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